NOTES ON THE LIFE CYCLE AND NATURAL HISTORY OF *PARIDES ARCAS MYLOTES* (PAPILIONIDAE) IN COSTA RICAN PREMONTANE WET FOREST*

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The *"Aristolochia*-feeding" swallowtails of the New World tropics comprise a well-known group of butterflies famous for their roles in mimicry complexes (Brower and Brower, 1964). Although the adult stages of many congeneric species of notable genera such as *Battus* and *Parides* have been known for some time (Godman and Salvin, 1879-1901; Seitz, 1924), there is considerably less information concerning the immature stages of these butterflies. This is particularly the case for the Central American species of *Parides,* one of the three genera (*Battus, Parides,* and the Old World *Troides*) of the Troidini, the tribe of pharmacophagous swallowtails (Ehrlich and Raven, 1965). While the Troidini are most abundant in the Old World tropics, it is apparent that New World genera in this tribe, such as *Battus* and *Parides,* have undergone extensive speciation in Central and South America. And with the exception of a few studies such as the recent study of *Battus polydamus* in Costa Rica (Young, 1971a) and another on the related *Ornithoptera alexandrae* on New Guinea (Straatman, 1971), the life cycles, behavior, and food plants of many species remain obscure. It is believed that the primarily neotropical distribution of the Aristolochiaceae (Pfeifer, 1966) is a major factor in accounting for the extensive adaptive radiation of *Parides* and *Battus* on these plants (Brower and Brower, 1964; Ehrlich and Raven, 1965).

It is the close and perhaps coevolutionary association of genera such as *Parides* with *Aristolochia* (in the Aristolochiaceae) and the co-occurrence of several sympatric congeneric species in lowland

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tropical forests (Young, 1971b) that makes these butterflies suitable candidates for the study of butterfly community structure in the tropics. In the Caribbean premontane wet forests of Costa Rica, there occur at least three species of *Parides* whose adults are often found together on the same flowers in forests: *P. arcas mylotes, P. childrenae,* and *P. sadyattes.* Another subspecies of *P. arcas,* namely *mycale,* is also seen in association with these species. As an initial approach to determining the ecological factors responsible for the co-occurrence of these similar species as a functional Müllerian mimicry complex (Young, 1971b), studies have been conducted on the life cycle, food plants, and other aspects of butterfly biology, for all of these species in Costa Rica. To date, the biological data for *P. arcas mylotes* (Bates) both in the laboratory (Young, 1972a) and field (Young, 1971b; 1972a) has been the most extensive for these species. This paper touches upon various aspects of biology in this species not covered in the previous studies. Other reports will subsequently appear concerning the biology of the remaining species. Godman and Salvin (1879-1901) mention that *P. arcas mylotes* is common in the Pacific and Caribbean lowlands of Central America, ranging from southern Mexico to Costa Rica. Thus the widespread geographical distribution of the butterfly throughout Central America makes it an even more attractive species to study from the standpoint of the effects of local selection pressures on natural history and life cycle.

Methods

The studies summarized here are: habitat selection, life cycle, larval food plant acceptance, and behavior of immatures and adults. Life cycle and larval food plant acceptance were examined in the laboratory, while the other studies were conducted in the field at two localities. At various times between late 1968 and mid-1970, field studies of *P. arcas mylotes* were conducted at Finca la Selva, a region of relatively undisturbed premontane tropical wet forest (elev. about 90 m) located on the confluence of the Rio Puerto Viejo and Rio Sarapiqui. During the months of July and August 1972, the butterfly was studied at Finca Tirimbina, a forest site located about 8 km west of Finca la Selva and at the basal belt transition zone (about 200 m. elev.) between montane and premontane tropical wet forest.

Habitat selection was studied by observing feeding and egg-laying activities of adults at various places in the forest, both at "La Selva" and "Tirimbina". At La Selva, habitat selection was studied spo-

radically several days each month over a 14-month period. At Tirim-
bina, it was studied systematically 14 days over a two-month period.

Life cycle studies consisted of the description of life stages and
the estimation of egg-adult developmental time under "laboratory"
conditions. These measurements were made on individuals reared
on a natural food plant, and eggs were obtained in one of two basic
ways. The first method was to collect eggs witnessed to be ovi-
posited in the wild; this method was employed primarily in the
Tirimbina studies and to a lesser extent in the earlier La Selva
studies. The second method was to obtain eggs by hand-pairing
newly-emerged adults, using the technique of Clarke (1952) for
Papilio machaon, or allowing mating to occur in pairs of adults
confined to plastic bags. The latter technique is useful to obtain
estimates of fecundity in this species (Young, 1972a). Both methods,
obtaining eggs in the wild, and mating females in the laboratory with
subsequent induction of oviposition, are very successful for this
species, provide large numbers of eggs for rearing studies. Combining
both methods, a large number of individuals were reared from La
Selva (primarily through the laboratory mating method) and a lesser
number were reared from Tirimbina. The "laboratory" for the La
Selva studies consisted of a well-ventilated room in an apartment in
San Jose, while the "laboratory" for the Tirimbina studies was a
room in a different apartment, located about 1.5 km from the first.
In both cases, air temperature usually varied between 21-23°C and
the humidity was about 45%.

The techniques for rearing immatures of this butterfly are given
in Young (1972a) for La Selva individuals, and essentially the same
methods were employed for the Tirimbina studies.

The larval food plant acceptance studies were conducted from
individuals obtained at Tirimbina during 1972. This study consisted
of offering first instar larvae immediately after hatching, in the
laboratory, fresh clippings of several species of *Aristolochia* from
various sources. The rationale was to offer separate small groups
of young larvae various species of *Aristolochia,* including species
known to be natural food plants. Larvae on each food plant were
then scored for survival rate and body size. There were five species
of *Aristolochia* that were called "novel" food plants in addition to
the two natural food plant species. Two experiments were con-
ducted in San Jose: in each of these, 12 larvae were reared on the
natural food plant and 13 were reared on each of two "novel" food
plants collected from different localities in Costa Rica. The remain-
ing three food plants were tested at Lawrence University during

September and October 1972. The three species of *Aristolochia* involved were already growing in a greenhouse tropical room for about two years, and the *Parides* eggs were transported (by air) from Costa Rica to Lawrence on September 6, 1972. Since the natural food plant was not in culture at Lawrence, enough cuttings of it were also brought to Wisconsin to sustain the larvae through the earlier instars. At Lawrence, 10 larvae were on the natural food plant, and 8 on each of the "novel" food plants.

Field studies of larval and adult behavior consisted of making repeated observations on the feeding, resting, and defensive habits of larvae in different instars, and on the oviposition behavior of adults.

RESULTS

Habitat selection

Adults of both sexes of *P. arcas mylotes* are most commonly encountered along paths, natural clearings, swamp edges, and other exposed areas that either border forest or those which are found in the forest interior. For example, the general study site at Tirimbina where adults were most frequently seen is between the edge of forest and a small river (Fig. 1). This small strip of dense secondary growth vegetation is the result of forest being cut back from the river edge for the original purpose of growing yucca and other vegetables that form the major diet of these people. Here, the adults fly low over dense second-growth vegetation, seldom crossing the small river, and frequently flying several meters into the shaded forest understory and canopy. Excursions into the forest were most frequently done by mated females in search of oviposition sites while males and very fresh (presumably unmated) females generally lingered in the sunlight second-growth. The strip of second-growth between the forest and river is a major courtship area for this butterfly at Tirimbina and extensive growths of the larval food plant vines are found hanging down from trees along the forest edge and growing horizontally in the canopy within a few meters from the edge. A later paper (Young, et al., in prep.) will demonstrate that mated females of this species are far more prone to dispersal than either males or unmated females. In the present paper, we can say that mated females cruise along extensive tracts of cleared forest edge in search of egg-laying sites, while males and unmated females remain close to their eclosion sites. Courtship encounters are generally confined to low sunlight vegetation very close to where the adults emerged from their pupae. Males precede females in emergence.

Fig. 1. A major habitat of adult *Parides arcas mylotes* (Bates) at Finca Tirimbina, near La Virgen, Heredia Province, Costa Rica. An adult population is found along the forest edge, and males are active in the low secondary growth vegetation between the forest and small river (Rio Tirimbina) to the left. August, 1972.

Thus habitat selection, which can obviously be exercised only by the adults (since eggs and larvae are relatively fixed through the oviposition strategy), is molded strongly in this species by two factors: (1) establishment of optimal courtship sites by males in sunlight second-growth bordering forests or forest clearings, and (2) the response by mated females to become more prone to disperse in search for oviposition sites. Similar adult movement patterns have been seen at La Selva, and the lesser vagility of individual males was mentioned in Young (1971b). A courtship strategy in which males patrol an area of the habitat consistently day after day (Young, et al., in prep.) and mate with females as the latter emerge from their pupae, is optimal for butterflies in which males are shorter-lived than females, as is the case with *Parides* (Young, 1972a). But Cook et al., (1971) report a short life expectancy of about 10 days in *P. anchises*

and *P. neophilus* in a seasonal habitat on Trinidad where torrent rains may kill off the adults of both sexes.

Although adult feeding preferences do not appear to be a major factor in dispersal patterns at Tirimbina, it is interesting to note that mimetic association with other species of *Parides* is most intense at nectaries at La Selva (Young, 1971b). At Tirimbina, *P. arcas mylotes* is the only species of this genus seen consistently at the study site, and flower specificity is not apparent. At La Selva, this butterfly as a functional component of Müllerian mimicry complexes exercise a strong preference to visit a single species of flower (*Hamelia patens*) also visited by other *Parides* (Young, 1971b); judging from the amount of time spent daily at *Hamelia* flowers, there appear to be very few or no other preferred adult food sources of *Parides* at La Selva. In the absence of the other *Parides* at the Tirimbina study site, adult *P. arcas mylotes* is found on a variety of flowers, usually ranging from red to purple. Thus in the absence of strong selection pressures favoring mimetic association, and where this mimicry is potentially most effective at a food source, flower specificity may break down for *Parides* in habitats where the species do not co-occur on a regular basis. Similar diurnal patterns of visitation at flowers between members of a tropical *Battus* mimicry complex in addition to the co-occurrence of several *Parides* at flowers at La Selva suggest strong selection pressures resulting in convergence of feeding habits to enhance mimicry (Young, 1971b; 1972b).

Although courtship activity is generally limited to the sunniest hours of the morning (Young, et al., prep.), adults of both sexes and various age-classes (distinguished by the extent of wing tattering) generally forage throughout the day, and they are relatively unaffected by changes in local weather conditions. Even at a montane tropical forest locality (Cuesta Angel) where a cloud forest occurs at about 1000 meters elevation, adults are seen foraging throughout the day at the bright red flowers of *Impatiens sultani* (Balsaminaceae — "Touch-me-nots"), a small herbaceous plant that is imported from Africa and that grows in large numbers. As the day becomes less bright in terms of illumination from the sun, these flowers become even more conspicuous due to increased contrast of the red coloration with the misty air; to the human observer, the flowers are more conspicuous, and perhaps the butterflies respond in a similar fashion. In both lowland and mountain localities, adult activity drops off sharply after about 4:00 P.M. When there is short succession of unusually dry days in both lowland and mountain

localities, adults, especially males, are frequently seen visiting receding mud puddles and moist patches of ground.

Life cycle and developmental time

The egg (Fig. 2-A-C) is deep rusty-brown and slightly flattened at the base. The diameter is 1.1 mm and the egg is covered with an irregular thick layer of an orange-red sticky substance, which attaches it to the leaf surface and gives the entire surface of the egg a rough appearance. This sticky substance forms thin threads which hang down from the upper half of the egg and assist in attachment (Fig. 2-A). It is not known if the sticky substance is also defensive in function, in the sense of discouraging attack by ants and other leaf-wandering predatory arthropods. The apical region of the egg darkens considerably immediately before hatching. Eggs are generally laid on the ventral surface of older leaves and occasionally in the crotches of small stems and petioles (Fig. 2-C). The amount or thickness of the sticky substance covering the eggs is apparently very variable, since other details of egg external morphology, such as deep grooves (Fig. 2-B, C) can be seen on some eggs while completely obscured on others. Eggs are laid singly but usually in loose clusters of 2-5 eggs on a single leaf.

At La Selva, the natural food plant is *"Aristolochia* sp." (this is a new species from northeastern Costa Rica soon to be described by H. W. Pfeifer based on my collection of it during March, 1970). At Tirimbina, the natural food plant is *Aristolochia constricta* Griseb. Both of these species occur in lowland forest on the Caribbean side of the central Cordillera in Costa Rica. Pfeifer (1966) mentions that *A. constricta* is a forest species found from Costa Rica to Panama, the Lesser Antilles, and probably northern South America.

The first instar is about 3.2 mm long when it hatches, and the ground color of the body is dark orange-brown. The head is shiny black. After the young larva begins to feed on leaf tissue, the body ground color becomes a deep wine red. All segments bear long tubercles of the same color as the body, but the lateral pair on the first segment are orange-white, and this color also characterizes the dorsal pairs of tubercles on segments two, seven, ten, and twelve (Fig. 2-D). The tubercles are fleshy for about one-third their length, with the apical two-thirds being stiff and bearing numerous tiny black spines (Fig. 2-D). The osmeterium is bright orange-yellow throughout larval life. By the time of the first molt, the larva is about 9 mm long.

Psyche
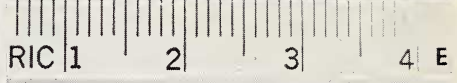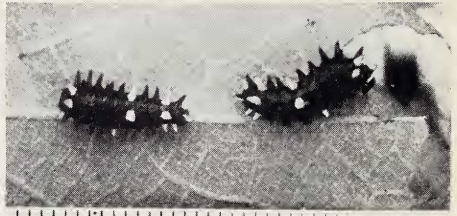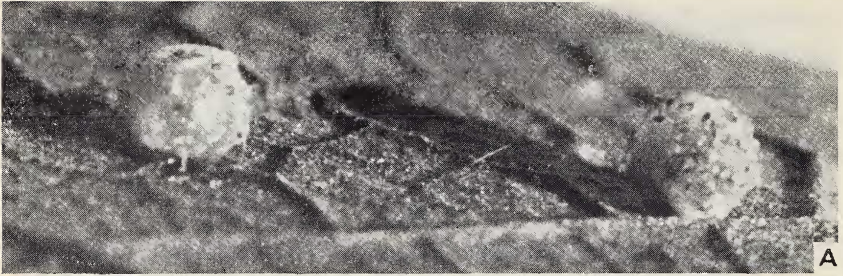
The second instar is remarkably similar in appearance to the first instar, with the only major difference being a loss of the spines seen on tubercles in the previous instar. The larva (Fig. 2-E, F) retains the six rows of spines of the first instar, in addition to the shiny black head and true legs. The precise arrangement of the tubercles is very noticeable in this instar. The first four thoracic segments bear two pairs of lateral tubercles, and the uppermost pair disappears until the tenth segment where it is resumed until the twelfth segment. The two pairs of lateral tubercles on these segments are not precisely in line: the tubercle of thoracic segment 1 are juxtaposed with those of thoracic segment 2 etc. The lateral tubercles of the thoracic segment 1 are considerably shorter than these tubercles on the remaining segments. The dorsal pair of tubercles on abdominal segments 1 and 4 are white, while the upper lateral pair of the fourth and fifth abdominal segments are also white. The highly reduced dorsal pair of the abdominal segment 11 are also white. This pattern of tubercle arrangement and coloration is retained throughout the rest of larval life. By the second molt, the larva is about 14 mm long.

The third instar is an exact replica of the second instar except that the ground color of the body is a very deep purplish black. The third instar is shown in Fig. 2-G. By the time of the third molt, the larva is about 23 mm long. The fourth instar (Fig. 3-A) is identical to the third instar except that the skin is very shiny and reflective. It attains a length of 35 mm by the fourth molt.

A dramatic change in the ground color occurs with the molt to the fifth instar (Fig. 3-B, C). The ground color is a dull, velvety purplish-brown mottled with irregular blotches of black. The black coloration is most extensive on the segments bearing white tubercles (Fig. 3-B, C). The white ridge along the anterior edge of the osmeterial cuff behind the head is more prominent in this instar. As this instar continues to grow, the ground color becomes even lighter in coloration as extensive velvety grayish-tan areas replace the formerly purplish-brown areas of the body. The coloration of the dark tubercles is also variegated during the fifth instar, with each tubercle bearing lines of white in addition to the mottled coloration of the

Fig. 2. Life cycle and behavior of *Parides arcas mylotes* (Bates). (A) dorsal view of two eggs on a leaf; note the rough surface and sticky strands on the eggs (B) single egg showing deep vertical grooves (C) single egg in crotch of stems (D) first instar, lateral view (E) two second instar larvae (one is feeding) (F) several second instar larvae living together (G) third instar, dorsal view.
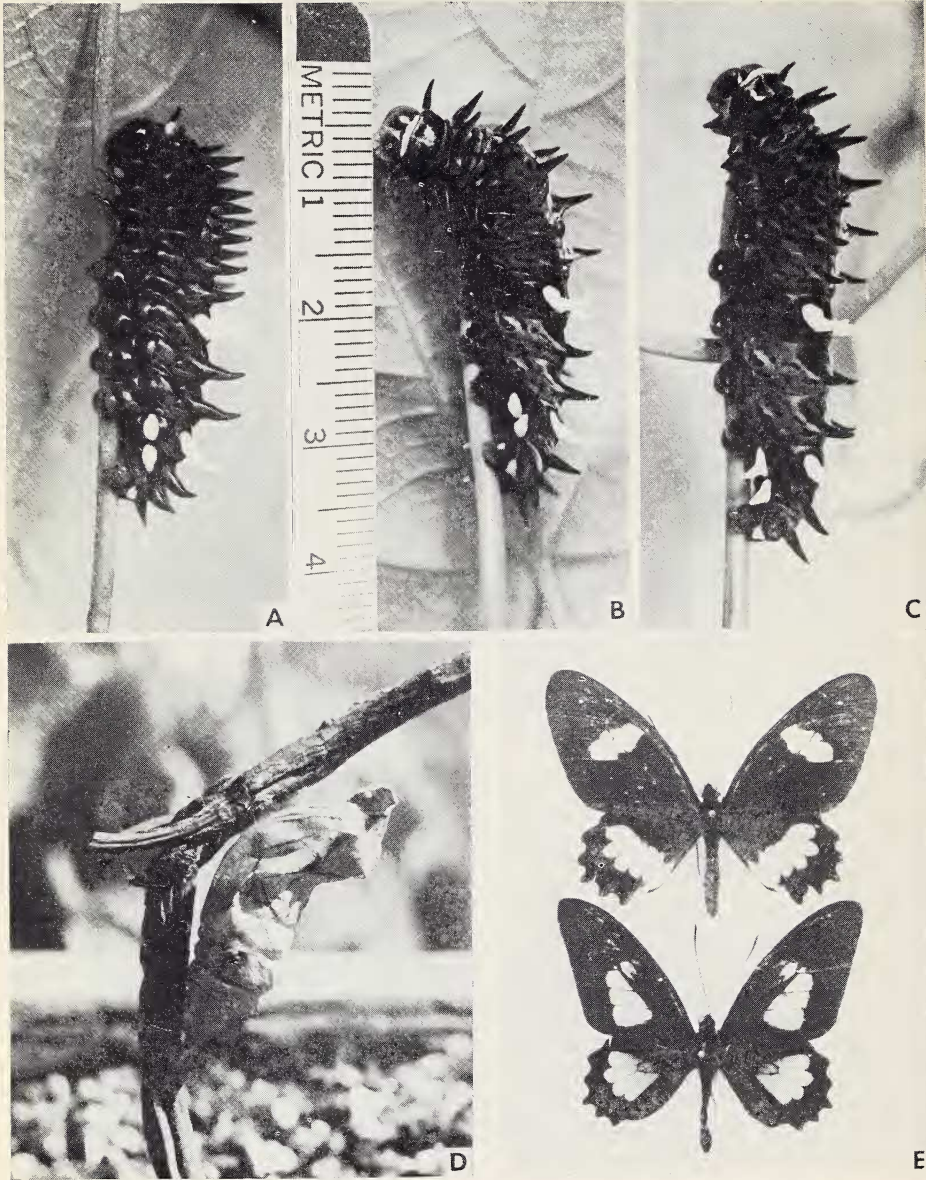
body ground color. By the time of pupation, the larva is about 45 mm long. The coloration of the larva remains unchanged at the time of pupation.

The pupa (Fig. 3-D) is about 25 mm long and the color pattern consists of various light shades of green and yellow. The frontal portions of the thorax and abdomen are yellow while the rest of the body is light green.

Godman and Salvin (1879-1901) and Seitz (1924) give good illustrations of wing color patterns of the adults (Fig. 3-E). The single light area of the dorsal surface of the forewing in the female is cream-colored while the dorsal bands on the hindwings are orange-red. This color pattern is very consistent in both laboratory-reared and wild-caught females of *P. arcas mylotes*. Less stable is the fore-wing dorsal coloration in the male within a single local population. The large spot on each forewing (Fig. 3-E) is light green but with the apical portion being cream-colored. Considerable variation is apparent in this "two-component" spot on the dorsal surface of the male's forewing; this variability concerns the presence, absence, and size of a second, very small two-component spot just inside the radial cell of each forewing, and almost touching the major spot (Fig. 3-E). Similarly, there is considerable variation in the discal cell spot. Godman and Salvin (1879-1901) mention the considerable variation in the forewing spotting pattern of male in the closely related species, *P. iphidamas*. Adults of both sexes of *P. arcas mylotes* can be distinguished from the subspecies *mycale* by the presence of a thin light red marginal border of the wings in the former subspecies, while these markings are white in the latter sub-species. The red patch on the dorsal surface of the hindwings in male *P. arcas mylotes* is more intense than in the female, and the distribution of the coloration is very different between the sexes (Fig. 3-E). In bright sunlight, the red patches of the male's hind-wing are often iridescent, giving off a purple lustre; this is not seen in the female. The mean length of the forewing in the female is about 40 mm, while the same statistic of the male is about 38 mm. Thus, not only is there a striking color sexual dimorphism in this butterfly, but also a consistent wing length difference between the sexes. In the absence of crowding, laboratory-reared individuals often

Fig. 3. Life cycle and behavior of *Parides arcas mylotes* (Bates). (A) fourth instar, lateral view (B) fifth instar, lateral view (C) fifth instar, feeding on the tip of a young stem of *Aristolochia* (D) pupa, lateral view (E) adults, female above, male below.

bear the same wing-length as wild-caught individuals from the same locality.

The egg-adult developmental time for *P. arcas mylotes* in the laboratory for individuals reared on *Aristolochia constricta* is summarized in Table 1. In a previous study (Young, 1972a), the egg-adult developmental time of this butterfly on *Aristolochia* sp. from La Selva was about 42 days. The developmental time in that study was measured on eggs obtained from La Selva adults. The developmental time for eggs obtained at Tirimbina and reared on *A. constricta* is 53 days (Table 1). This difference in developmental time between the two populations is apparent in eggs, larvae, and pupae: the egg stage lasts 4 days in La Selva individuals as opposed to 6 days in Tirimbina individuals; the total larval period for La Selva individuals is 17 days as opposed to 33 days in Tirimbina individuals; the pupal stage lasts 21 days in La Selva individuals as compared to 14 days in Tirimbina individuals.

Larval food plant acceptance

Development from the egg stage on natural food plants is successfully completed in the laboratory (Young, 1972b; Table 1). When other species of *Aristolochia* are tested, differences in food plant acceptance by the larvae become apparent. Development is successfully completed, and without a change from the Tirimbina developmental time when larvae are reared from the egg stage on *Aristolochia labiata* Willd. in Costa Rica. But larvae die during the first instar when offered *A. veraguensis* Duchr. in Costa Rica. For

TABLE 1. The developmental time of *Parides arcas mylotes* on a natural food plant, *Aristolochia constricta,* under laboratory conditions.*

	EGG	INSTAR 1	INSTAR 2	INSTAR 3	INSTAR 4	INSTAR 5	PUPA	TOTAL EGG-ADULT
MEAN DURATION (DAYS)	6	5	5	6	6	11	14	53
± S.E.	± 0.1	± 0.3	± 0.5	± 0.3	± 0.2	± 0.8	± 0.2	
N	46	46	42	42	40	37	37	

*Laboratory conditions consisted of confining larvae to closed plastic bags containing clippings of food plant. Physical conditions around the bags were 21-23°C and about 45% relative humidity. See text for further details of rearing techniques, laboratory conditions, etc.

the rearing studies at Lawrence, all the larvae died either in the first or second instar when reared on *A. ringens* Vahl, *A. littoralis* Parodi, and *A. gigantea* (Mart. & Zucc.). For the groups of larvae offered these species, survivorship was 0%. Thus, in addition to the two known natural food plants of *P. arcas mylotes,* namely *Aristolochia* sp. from La Selva and *A. constricta* from Tirimbina, the butterfly only feeds successfully on *A. labiata* Willd. in Costa Rica.

Behavior of adults and larvae

Observations on adult behavior are limited to the oviposition strategy of this species, since a later report (Young et al., in prep.) will discuss other aspects of adult behavior, most notably, the spacing patterns of males and females, and the courtship strategy.

Adults of both sexes generally cruise very low over second-growth vegetation. Mated females in search of oviposition sites exhibit extreme forms of cruising behavior in two ways: (1) they perform sudden, almost vertical darts into the canopy where *Aristolochia* lianas are found, and (2) they flutter through very dense second growth within a few inches of the ground, and often being obscured from view for several minutes.

Such patterns of cruising behavior by egg-laying females are consistent with the observation of well-developed food plant specialization in this butterfly. The usual situation locally is that eggs are laid on a single species of *Aristolochia,* and there is considerable site-selectivity exercised in terms of placing the individual eggs securely on the older leaves of an individual plant. The eggs are seldom laid on young leaves and occasionally on stems at crotches between two stems. Eggs are customarily laid on the dorsal surface of older, well-shaded leaves of the vine, and anywhere from one to five eggs may be laid in a loose cluster in this manner. Upon landing on a leaf for oviposition, the female exhibits considerable wing fluttering and drumming behavior with the antennae; an egg is usually laid within 12 seconds. Oviposition is most commonly seen during sunny hours throughout the day. While males may be cruising in the general vicinity of egg-laying females, there is virtually no observable interactions between the sexes. The less cohesive nature of the mated female portion of a local breeding population of *P. arcas mylotes* (Young et al., in prep.) results in there usually being no more than one or two ovipositing females at a larval food plant patch on a given day. These individuals cover large tracts of habitat in searching for oviposition sites, but usually return repeatedly on the same day to a given food plant patch.

While clustering of eggs in the field is generally loose and vari-

able, when mated females of this butterfly lay eggs in the laboratory, there is usually a tight clustering of eggs (Young, 1972a). Thus tight clustering of eggs (the arrangement of eggs into a group where the eggs touch each other) can be induced in the laboratory when females are confined individually or in low numbers to plastic bags containing clippings of the food plant. Such clustering, however, is seldom found in the wild in this butterfly and other species of *Parides*.

The larvae of *P. arcas mylotes* exhibit several behavioral patterns that warrant more intensive study. Upon hatching the larva invariably eats its emptied egg shell, and then moves a considerable distance to the closest youngest leaves. Locomotor movement is accompanied by the production of silken treadwork on which the larva crawls from one place to another. Although small groups of larvae are frequently found in the field (Fig. 2-E, F) there is no evidence for gregarious habits among the individuals in a group. All individuals on an individual vine generally feed at the same times of day, but there is no indication of coordinated locomotor movements among the individuals. Furthermore, single or doublets of larvae are also frequently encountered in the field. Larvae of all instars are generally inactive at night. The extent of larval dispersion when several eggs are laid on a vine may be governed by the size of the vine. For example, it is not uncommon to find one or two fourth or fifth instar larvae present on a young vine (1-2 m tall) in the field, and in cases where there are two present, these individuals are often found together on the same stem. Both in the field and laboratory, older larvae eat the stems of young *Aristolochia* vines (Fig. 3-C). On very large vines in which woody tissue is well-developed, older larvae are generally confined to feeding on leaves and it is unusual to find two or more individuals resting close together. Group formation is frequently encountered only in the younger larvae (first and second instars) and in cases where larger (older) larvae are clumped, this is most likely due to the fact that they are feeding on a young vine and the food supply is limited. It is not known if *Parides* larvae crowded on young *Aristolochia* vines will leave the vine in response to intense crowding. The osmeteria of the larvae of swallowtail butterflies are functional defense organs. Predatory attack on the larvae of *P. arcas mylotes* in the wild has not been observed to date. The defensive strategy of the larvae against predators includes (1) possession of conspicuous body coloration in which the dark body and pattern of white tubercles stands out against the light green coloration of *Aristolochia* leaves, (2) possession of an apparently

functional and brightly-colored defensive organ, the osmeterium, and (3) probably the possession of generally toxic or poisonous systemic properties making the insect unpalatable, since they feed on vines reputed to have very toxic properties.

Discussion

Young (1971a) reported a developmental time for *Battus poly-damus* on *Aristolochia veraguensis* of about 14 days under similar laboratory conditions to those employed in the present study. Straatman (1971) reported the developmental time of *Ornithoptera alexandrae* Rothschild to be 131 days on *Aristolochia schlechteri* and 107 days on *A. tagala*, where the difference occurred during the larval period. The developmental time of *Parides arcas mylotes* on *Aristolochia* sp. from La Selva is 42 days (Young, 1972a) while 53 days on *A. constricta* (Table 1.). Furthermore, the developmental time of *Parides childrenae* on *Aristolochia pilosa* at La Selva is about 42 days (Young, 1972a). Thus different genera in the Troidini have different developmental times on different species of *Aristolochia*. At La Selva there has been ecological divergence between *P. arcas mylotes* and *P. childrenae* with respect to the species of *Aristolochia* used for oviposition and larval food-consumption. Furthermore, two different strains of *P. arcas mylotes* are evolving between La Selva and Tirimbina: the duration of all immature life cycle stages has been altered and the species feeds on a different species of *Aristolochia* at each locality. If this difference in developmental time was due solely to differences between the larval food plant species, we would expect to find only a change in duration of the larval period similar to that noted by Straatman (1971) in *Ornithoptera alexandrae* on New Guinea. But in the case of *P. arcas mylotes*, there has been a change in the embryonic and post-embryonic developmental time which suggests genetic alterations. Strain-effect is not solely confined to food plant differences of the type noted for *Victorina epaphus* on the Pacific and Caribbean slopes of the central Cordillera in Costa Rica (Young, 1972c). Precisely what sorts of ecological factors are reshaping the developmental architecture of *P. arcas mylotes* at different localities on the Caribbean drainage of the central Cordillera in Costa Rica remain obscure at this time. One interesting hypothesis concerning this question would focus on a higher level of predation pressure on eggs and larvae in La Selva populations of the butterfly, which would favor an accelerated developmental period for these life stages.

The inability of young larvae of *P. arcas mylotes* to survive on *Aristolochia ringens, A. littoralis, A. gigantea,* and *A. veraguensis* may be due to the lack of evolutionary contact (Ehrlich and Raven, 1965) with these plants. An alternative explanation is that extreme food plant specialization in the butterfly has resulted in the narrow restriction to only a few species of *Aristolochia* locally. Until more is known about the regional and geographical distribution of various species of *Aristolochia* in Central America, it will be difficult to resolve the question of larval food plant adaptability in *Parides*. Unfortunately eggs from La Selva have not been reared on *A. constricta* from Tirimbina nor the converse, namely, eggs from Tirimbina reared on *Aristolochia* sp. from La Selva.

The question of unpalatability is of considerable ecological and evolutionary interest. Brower and Brower (1964) have demonstrated that freeze-killed adult *Parides neophilus* L., which feeds on various species of *Aristolochia* on Trinidad, are very unpalatable to Scrub Blue Jays in the laboratory. Brower and Brower (1964), Ehrlich and Raven (1965) and Pfeifer (1966) cite previous studies which illustrate the toxic properties of various compounds derived from the vegetative portions of Aristolochiaceae. The question of palatability in genera of the Troidini (*Parides, Battus, Ornithoptera,* and *Troides*) is of interest since the larvae are presumably unpalatable in addition to possessing a defensive organ (Eisner et. al., 1971). The larvae of these genera, as exemplified in the present study by *P. arcas mylotes,* are generally conspicuous in appearance (Fig. 2, 3) to the human observer.

The possession of a dual system of defense by *Parides* larvae and other troidines is related to the functional responses of each component (unpalatability and chemical defense secretion) to different kinds of predators that the larvae encounter in their habitats. Unpalatability, as evidenced here by the conspicuous coloration of the larvae and the toxic properties of their food plants, is an adaptation for defense against vertebrate predators such as insectivorous birds, mammals, and reptiles. Brower and Brower (1964) have demonstrated that blue jays become ill after eating an unpalatable butterfly and that there is a subsequent modification in prey-selection behavior by such an experienced predator to avoid the prey on further visual contact with it. Thus, the flexible learning abilities of vertebrate predators makes unpalatability an effective defensive mechanism that increases the likelihood of survival of individuals in a prey population. An insectivorous bird foraging in forest edge second-growth or forest canopy has daily opportunity for visual contact with the

poisonous *Parides* larvae which stand out against the foliage back-
ground during the day time when they are feeding. This is an ideal
situation for unpalatability to be effective against vertebrate preda-
tors. The bird does not have to make tactile contact with the poten-
tial prey, but can recognize it from a distance. On the other hand,
the added possession of a defensive organ that produces a volatile
chemical secretion would be an adaptation primarily against inverte-
brate (arthropodan) predators that make tactile or very close visual
contact with *Parides* larvae and elicit a behavioral response. Such a
defensive mechanism would be essentially ineffective against verte-
brate predators since the larvae could not respond fast enough to the
strike of the predator, and the larva would invariably be killed.
This is especially true since lepidopterous larvae have low visual
sensing ability but quick discriminatory ability for tactile stimuli.
In a similar fashion, the generally instinctive nature of the be-
havioral repertoire of invertebrate predators would make unpalata-
bility an ineffective defense mechanism against these predators.
Under such conditions, there is strong selection for the evolution with
a dual system of defense, one adapted to vertebrate predators with
developed learning abilities (unpalatability), and the other adapted
to smaller invertebrate predators with instinctive behavior patterns
(defense glands). Furthermore, the larvae would probably survive
single attacks by invertebrates such as ants, even though the in-
stinctive nature of the predator's behavior results in repeated attacks
on the prey. The small size of invertebrate predators and the ability
of *Parides* larvae to survive individual attacks (in the form of small
bites) reduces the threat of death from instinctive predatory be-
havior patterns. Thus, in the absence of conclusive evidence, I sug-
gest that the unpalatable properties of troidine butterfly larvae (Euw
et al., 1968) are an adaptation to potential large vertebrate preda-
tors, while their defensive organs comprise an adaptation to inverte-
brate predators. This effect is even more pronounced in the adults,
which are very unpalatable to birds (Brower and Brower, 1964),
since there are ample opportunities for foraging birds which catch
insects on the wing to recognize, at a distance, the butterflies through
conspicuous coloration. Therefore, adult butterflies should possess
unpalatability rather than defensive gland as an adaptive strategy
against vertebrate predators. The studies of Euw et al. (1968) and
Eisner et al. (1971) indicate that unpalatability and chemical de-
fense secretions in troidine butterflies are due to very different kinds
of chemical compounds.

The oviposition behavior varies greatly for different genera of

troidine butterflies. Straatman (1971) found that *Ornithoptera alex-andrae* lays eggs singly, and Cook et al. (1971) comment that single oviposition also occurs in *Parides neophilus* and *P. anchises* on Trinidad. But Young (1971a) found tight cluster oviposition in the field to prevail in *Battus polydamus* in Costa Rica. The oviposition in *P. arcas mylotes* is very variable since eggs may be laid singly or as loose clusters of varying numbers of eggs per cluster. But oviposition in the wild is never tightly clustered as seen in *Battus polydamus* (Young, 1971a). The *P. arcas mylotes* pattern is basically single, but with a behavioral tendency to lay several eggs close together on a single leaf. This behavior results in first and second instar remaining together in small groups and dispersing later, which is very different from the more well-defined gregarious behavior exhibited by the larvae of *Battus polydamus* (Young, 1971a). Larvae in the latter case are generally gregarious through all instars and presumably fitness is increased as noted in other studies (Ghent, 1960). A similar oviposition pattern to that found in *P. arcas mylotes* also occurs in *P. childrenae* and *P. sadyattes* (Young, in prep.). Thus the oviposition pattern of *Parides* in Costa Rica (and perhaps for all of the Central American mainland) is a variable one being basically single but typified by loose clusters of a variable number of eggs, usually ranging between two and five on a leaf. It is clearly not entirely single, nor is it the tight-clustering pattern seen in *Battus*. As might be predicted, the larvae are semi-gregarious in *P. arcas mylotes* (Fig. 2-E, F) as well as in *P. childrenae* and *P. sadyattes* (Young, in prep.) and perhaps in most *Parides,* while truly gregarious in *Battus*. These preliminary findings in different species suggest that there may exist distinct phylogenetic patterns of type of oviposition and extent of larval gregariousness at the generic level in the Troidini, and perhaps within other tribes of Papilioninae. Superimposed upon evolutionary history will be the prevailing ecological conditions (Birch and Ehrlich, 1967) such as food plant specialization, patchiness of food plant populations, predation pressure on immatures, adult population cohesiveness, and several others, which mold the oviposition strategy in either direction (single versus clustering) and the likelihood of larval gregarious behavior.

Summary

In this paper concerning the life cycle and natural history of *Parides arcas mylotes* (Bates) on the Caribbean side of the central Cordillera in Costa Rica, the following points were emphasized:

(1) The butterfly is a forest species which is most commonly encountered along forest edges associated with extensive borders of secondary growth vegetation or small forest clearings.

(2) Habitat selection by adults is governed primarily by two factors: (a) the selection of optimal courtship sites by males exhibiting home range behavior, and (b) the search pattern of mated females for suitable oviposition on *Aristolochia* vines along forest borders and in the canopy.

(33 The larvae of this species are probably warningly-colored, since they contrast greatly with the light green leaves of the food plant. The pupae are cryptically colored against the same background.

(4) The egg-adult developmental time varies on different natural food plants in different localities: on *Aristolochia* sp. from Finca La Selva the developmental time is about 42 days; on *A. constricta* from Finca Tirimbina 53 days. This difference is due to more than food plant difference since the egg stage is considerably shorter in individuals reared on *Aristolochia* sp. There appears to have been the evolution of different strains in different localities where different food plants are also exploited.

(5) Development is successfully completed on *A. labiata* but unsuccessful on *A. veraguensis, A. ringens, A. littoralis,* and *A. gigantea.* The inability of young larvae to feed on these species may be due to either (a) a lack of contact with those species, or (b) the development of narrow food plant specialization.

(6) The conspicuous coloration (contrast) of the larvae against the light green food plant leaves and the known toxic properties of the Aristolochiaceae indicate that the larvae are unpalatable to vertebrate predators with well developed learning abilities. The unpalatability of the larvae is inferred from the known unpalatability of the adults of a related species of *Parides.* The possession of an osmeterial defensive organ is interpreted here, on the other hand, as being primarily an adaptation of defense against invertebrate (arthropodan) predators with rather inflexible (instinctive) learning abilities.

(7) The variable oviposition strategy of *P. arcas mylotes* in the wild is not strictly single nor is it clustering. Eggs are generally laid in loose clusters of two to five eggs on a leaf, and this pattern appears to be a modified form of single oviposition. When mated females are confined to plastic bags in the laboratory, tight clustering of eggs can be induced. Previous studies show that at least one tropical species of *Battus* lays eggs in tight clusters in the wild,

while some species of *Parides* undoubtedly lay eggs singly and *Ornithoptera* lays eggs singly. It is suggested that there may exist phylogenetic differences in oviposition patterns at the generic level in the Troidini, and that secondary differences in these patterns are molded by contemporary ecological factors.

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